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A New Mollusk (Bivalvia, Erycinidae) Commensal on the Stomatopod Crustacean *Lysiosquilla*

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INTRODUCTION

Certain small bivalve mollusks, most frequently members of the eulamellibranch superfamily Erycinacea, are often associated with other marine invertebrates as parasites, symbionts, or commensals. Pelseneer (1935) and Caullery (1952) have listed numerous leptonids, erycinids, galeommatids, and montacutids which live in or attached to coelenterates, sipunculids, crustaceans, echinoids, holothurians, or mollusks. In North America known examples of these interrelationships include: *Rocheportia cuneata* in association with the sipunculid worm *Phascolion strombi*, in the empty shells of *Nassarius trivittatus* or *Eupleura caudata* (Hampson, 1964); *Rocheportia* sp. commensal on specimens of the large sand crab *Blepharipoda occidentalis* (Burch and Burch, 1944; Emerson, 1944); *Serridens oblonga* on the chiton *Ischnochiton heathiana* (Smith and Gordon, 1948); and *Pseudopythina rugifera* attached to the blue mud shrimp, *Upogebia pugetensis* (Dall, 1899), or, even more frequently, to the sea mouse *Aphrodite* (MacGinitie and MacGinitie, 1949).

From the burrows of the stomatopod crustacean *Lysiosquilla maculata* in Australia, Popham (1939) has described the commensal galeommatid

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Phlyctaenachlamys lysiosquillina, and Powell (in Morton, 1957) has suggested that the small New Zealand bivalve *Divariscintilla maoria* may live associated or attached to *Lysiosquilla*. Holthuis (1951) has reviewed the taxonomy and literature on the small lamellariid gastropod *Caledoniella montrouzieri*, which is known to associate with the stomatopod *Gonodactylus chiragra*.

During the preparation of a revision of the Stomatopoda, Dr. Raymond Manning of the United States National Museum of the Smithsonian Institution noted several specimens of a small, attached bivalve on a specimen of the Caribbean *Lysiosquilla scabricauda* (Lamarck) in the collection of the American Museum of Natural History. This discovery constituted the first documented occurrence of a commensal lamellibranch attached to the ventral surface of the abdomen and thorax of a stomatopod and, on close examination, the small bivalve proved to be a new genus and species.

PARABORNIA, NEW GENUS¹

TYPE SPECIES, HERE DESIGNATED: *Parabornia squillina* Boss, new species.

DESCRIPTION: Shell small, with a weak amphidetic external ligament and a developed, central, internal resilium, which lacks a lithodesma. Dentition consisting of two small dentiform processes on each side of resilium; denticles of right valve interlocking between those of left valve. Narrow, ventral, pedal-byssal gape and obsolete anterior and posterior gapes. Mantle papillose, with slitlike posterior and broad anteroventral openings. Both ctenidia with complete inner and outer demibranchs. Foot divided into anterior pedal and posterior byssal portions. Full complement of adductor and pedal-byssal musculature developed. Sex and incubatory behavior unknown.

Parabornia squillina, new species

Figures 1-3

DESCRIPTION: Shell small, extending to less than 7 mm. in length and to less than 5 mm. in height, compressed, lentiform, equivalved, inequilateral, thin, fragile, subtransparent, and whitish. Umbos anterior to middle, elevated, inflated, prosogyrous, and with a moderately extensive internal cavity. Anterior portion of shell shorter than posterior. All margins smoothly convex; anterior margin broadly rounded; posterior margin somewhat narrowly round and pointed. Appressed valves with a

¹ This generic name is feminine and is compounded of *Bornia* Philippi and the prefix "para," meaning "alongside."

narrow, ventral, pedal-byssal gape and obsolete anterior and posterior gapes. Shell sculptureless, with faint, microscopic, subreniform, concentric lines of growth evident in transmitted light. No true lunule or escutcheon. Adductor, pedal, or pallial muscle scars not impressed or visible. Hinge line gently convex, consisting of a weak, obsolete, amphidetic, external ligament and a developed, buttressed, internal resilium without a lithodesma. Dentition weak, centralized, subumbonal, and consisting of two small teeth or denticles in both valves; resilium uniting valves between paired teeth. Right denticles somewhat pointed, narrowly divergent, and interlocking between blunt, more widely divergent left denticles. Mantle united dorsally, posteriorly, and posteroventrally but with a single, posterior, anal, or exhalant slit and an anteroventral pedal-byssal and

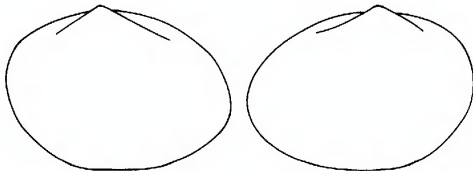


FIG. 1. Outline of the external surface of the shell of *Parabornia squillina*, new species. *Left*: Left valve. *Right*: Right valve. Length of specimen, 5.9 mm.

inhalant opening. Mantle edge with numerous papillae which are differentiated anteriorly into three tentaculate structures but not differentiated posteriorly. Mantle capable of complete retraction into shell cavity. Ctenidia consisting of two laterally paired demibranchs with ascending and descending lamellae, the external demibranch smaller. Foot terete in section, weakly grooved, plantar, and with a well-developed byssal gland posteriorly. Anterior and posterior adductor muscles subequal in size; anterior and posterior pedal retractors dorsal to adductors. Sex and incubatory behavior, if any, unknown.

LENGTH	HEIGHT	WIDTH	
5.9 mm.	4.2 mm.	1.8 mm.	Holotype
6.3	4.5	2.0	Paratype
6.2	4.3	—	Paratype
6.1	4.2	1.8	Paratype
6.0	4.2	1.8	Paratype
6.0	4.2	1.8	Paratype
5.8	4.2	1.8	Paratype
5.7	4.2	1.8	Paratype
5.6	3.9	—	Paratype
4.7	3.6	1.4	Paratype
4.5	3.1	1.4	Paratype

TYPES: The holotype (A.M.N.H. No. 112526) is preserved in the

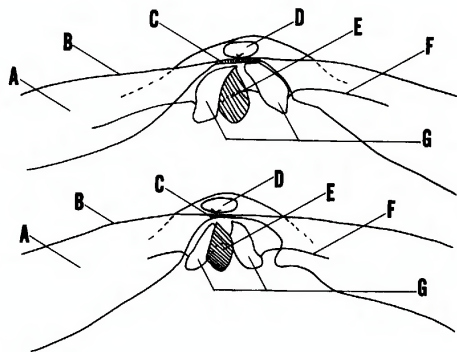
Department of Living Invertebrates in the American Museum of Natural History. Eight paratypes (A.M.N.H. No. 112527) are also deposited in the American Museum. Two paratypes (U.S.N.M. No. 653701) are deposited in the United States National Museum of the Smithsonian Institution.

TYPE LOCALITY: The type locality is Cristobal, Canal Zone, Panama. The specimens were collected on August 23, 1934, attached to the ventral surface of the abdomen and thorax of *Lysiosquilla scabricauda* (Lamarck).

ANATOMICAL REMARKS (SEE FIG. 3): The mantle has two openings, a small posterior exhalant slit and an extensive anteroventral gape which is functionally a pedal, byssal, and anterior inhalant opening. The inner lobes of the mantle fuse ventrally just posterior to the position of the byssus

FIG. 2. Hinge of *Parabornia squillina*, new species. *Top*: Left valve. *Bottom*: Right valve. Length of area illustrated, about 2 mm.

Symbols: A, reflected portion of the periostracum; B, edge of the shell; C, obsolete external ligament; D, umbo; E, internal resilium; F, lateral buttress of the hinge plate; G, denticles.



and anterodorsally in the vicinity of the anterior adductor muscle. There are three mantle lobes: a thin outer lobe which secretes the periostracum and lies next to the inner surface of the shell at its edge; a middle, thickened, muscular lobe; and a thin inner lobe which is fused along much of its extent and which bears numerous papillae on its outer surface. The papillae extend completely around the margin of the mantle, even dorsally where they are small. Anteriorly, just at the fusion of the inner lobe of the mantle near the anterior adductor muscle, there are three pairs of differentiated, enlarged, elongate papillae or "tentacles." There are no other differentiated papillae.

The foot is elongate, bluntly pointed anteriorly, and broadly terete in cross section. Its ventral surface is lightly grooved in the anteroposterior plane. The extensive and well-developed byssal gland and groove occupy the posterior portion of the foot.

The ctenidia consist of two pairs of demibranchs which are united posteriorly behind the foot. Both demibranchs have ascending and descending lamellae, and the gill filaments are numerous and lack inter-

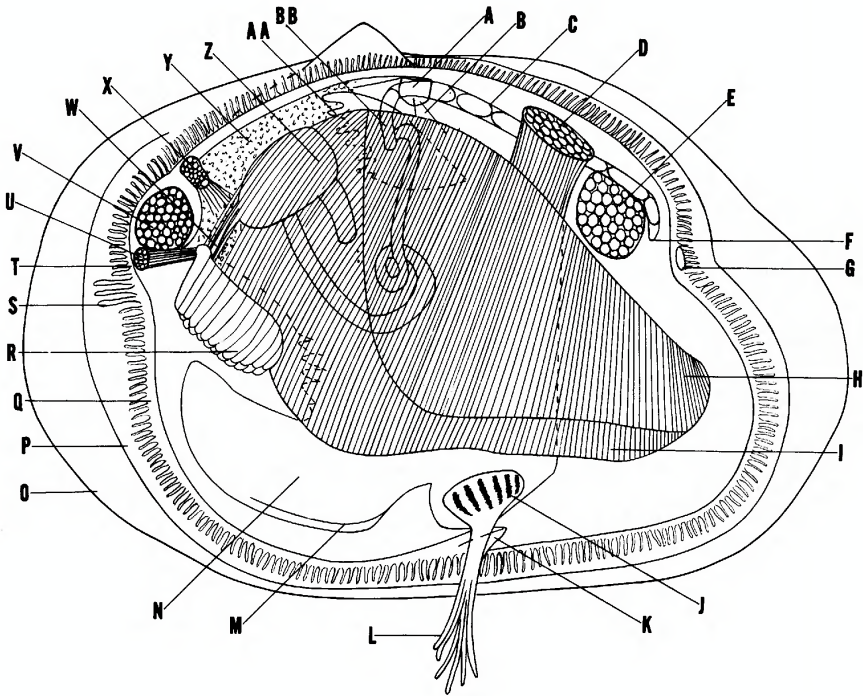


FIG. 3. Semidiagrammatic illustration of the anatomy of *Parabornia squillina*, new species. Specimen with the left valve removed to show general structural features. Length of specimen, about 6 mm.

Symbols: A, ventricle; B, auricle; C, rectum; D, posterior pedal-byssal retractor muscle; E, posterior adductor muscle; F, anus; G, exhalant slit; H, outer demibranch; I, inner demibranch; J, byssal gland; K, ventral union of the inner lobes of the mantle; L, byssus; M, pedal groove; N, foot; O, outer lobe of the mantle; P, muscular lobe of the mantle; Q, inner lobe of the mantle, with papillae; R, labial palp; S, differentiated papillae; T, anterior union of inner lobes of the mantle; U, anterior pedal protractor muscle; V, anterior adductor muscle; W, esophagus; X, anterior pedal retractor muscle; Y, digestive gland; Z, stomach, with the style sac; AA, gonad; BB, intestine.

filamentar junctions. The inner demibranch is more extensive than the small and somewhat reduced outer demibranch. There are two pairs of moderately sized, rectangularly shaped labial palps which are fused anteriorly to form the lips of the mouth. The anterior ventral edge of the inner demibranch lies between the inner and outer palps in a position similar to that figured by Popham (1939) for *Kellia suborbicularis*.

The muscular system is well developed and isomyarian. The posterior adductor is broadly sublunate, while the anterior adductor is subtrigonal.

A strong posterior pedal-byssal retractor muscle inserts on the shell just anterodorsal to the posterior adductor, while a smaller anterior pedal retractor attaches just posterodorsal to the anterior adductor. The small, thin, pedal protractor arises ventral to the anterior adductor. The muscle system of *Parabornia* is similar to that of *Bornia* as described by Deroux (1961).

The alimentary canal consists of a slitlike mouth, a rather elongate esophagus, a large stomach, with a posteriorly extending style sac surrounded by the digestive gland, a doubly looped intestine which is not united with the style sac, a rectum which traverses the heart, and an anus which terminates just dorsal to the exhalant opening. Fecal pellets are contained in the rectum. The kidney lies between the heart and the posterior adductor muscle and is traversed by the posterior pedal-byssal retractor muscle. The heart is enclosed in an extensive pericardial cavity; the auricles are paired, transparent, and oblique; the ventricle surrounds the rectum, and a dorsal aorta extends anteriorly. No definitive pericardial gland was observed. The glandular, tubulous, and white gonad is anteroventral to the pericardial cavity and covers a portion of the intestinal tract. It is probable that the specimens dissected were males, in which case the species would be dioecious, but for lack of positive evidence it is not possible to say whether the species is monoecious or dioecious. Likewise it is impossible to say whether the species is incubatory. Although no young were found in the mantle cavity, reproduction could occur at a time other than when the specimens were collected.

A developed cerebropleural ganglion is situated near the posteroventral surface of the anterior adductor muscle, and a bilobular visceral ganglion is between the pedal-byssal retractor and the anteroventral surface of the posterior adductor muscle; the pedal ganglia were not observed.

DISCUSSION OF SYSTEMATIC PLACEMENT: The relationship of *Parabornia* to other small commensal bivalves is not easily determined. Convergence and parallelism in morphological traits, both anatomical and conchological, contribute significantly to the difficulty of discerning a natural taxonomic system which reflects the phylogeny of the group. Dall (1900) and Cossmann and Peyrot (1912) presented critical discussions of the numerous generic and subgeneric divisions based primarily on the characteristics of the hinge and dentition. Pelseneer (1909, 1911, 1925) differentiated the families of these specialized bivalves, indicated the relative positions of genera, and showed where some convergence of types existed. Essentially Thiele (1935) and Popham (1939, 1940) followed Pelseneer in their discussions of the anatomical characteristics of certain families, and Kautsky (1939) based his classification on the outline of

Thiele. More recently, Chavan (1960) has presented a critical discussion of the hinge mechanisms of these mollusks and has discerned six families in the Erycinacea.

To identify the relative taxonomic position of *Parabornia*, an approach that combined the conchological data of Chavan (1960) and the anatomical detail of Pelseneer (1911) and Thiele (1935) was employed. The dentition of *Parabornia* (fig. 2) consists of a central hinge plate with subtending, thin, lateral buttresses. The hinge plate itself supports the internal ligamental element or resilium. On each side of the internal ligament there are small protuberant denticles. In the right valve, the denticles are narrowly divergent and rather pointed, with a tendency to become somewhat lobate distally. In the left valve, the denticles are blunt, oblong, and more widely divergent. The denticles of the right valve interlock between those of the left valve, and the resilium connects the valves within the area of the denticles of the right valve. Such a dental configuration falls within Chavan's "*lucinoide ancien*" type, exemplified by the family Montacutidae. Chavan included within this family a typical group that has only lateral lamellae, represented by *Montacuta* and *Devonia*, another group with short, dentiform lamellae, with *Tellimya*, *Pythinella*, *Laubriereia*, *Lasaeonaera*, *Rochefortula*, and a third group with *Kelliopsis*, *Orobitella*, and *Decipula* which has the anterior lamella coiled up at its extremity, producing a non-detached, toothlike structure. Additionally, *Kona*, *Malvinasia*, and *Mysella* are related to the third group. *Parabornia* appears to be most similar to the group represented by *Tellimya*, that is to say, the division that has short, dentiform lamellae. *Tellimya* was included by Thiele in the Erycinidae rather than the Montacutidae.

There is a general lack of agreement or concordance of interpretation among the major authors on the position of certain genera in families and subfamilies of the Erycinacea. At one time, the superfamily Cyamiacea, including such genera as *Cyamiomactra* and *Sportella*, was included in the Erycinacea. Members of the Cyamiacea possess two posterior mantle openings which act as inhalant and exhalant siphons, while the Erycinacea, on the other hand, have only a single posterior exhalant mantle opening, with the inhalant opening anteriorly. Accordingly, Thiele (1935) separated these distinct superfamilies as did Franc (1960) who used the names Cyamioidea for the Cyamiacea and Leptonoidea for the Erycinacea.

Parabornia possesses a single, posterior, exhalant, siphonal slit and an extensive anterior mantle opening which functions as the pedal-byssal as well as the inhalant orifice. Thus it is not cyamiacean but erycinacean in its affinities. In life, the probable direction of water flow through the

mantle cavity of *Parabornia* is from the anterior mantle opening toward the short, posterior, exhalant mantle slit, a so-called primitive molluscan condition (Popham, 1939).

Thiele (1935) recognized two families in the Erycinacea, namely, the Ercinidae, with both inner and outer demibranchs in a ctenidium, and the Montacutidae, with only a single demibranch per ctenidium. *Parabornia* has two complete right and left ctenidia, with the outer demibranchs somewhat reduced; it therefore belongs within the Erycinidae of Thiele. Further, four subfamilies, the Erycininae, Leptoninae, Galeommatinae, and Chlamydoconchinae, comprise the Erycinidae according to Thiele, and, by the process of elimination, *Parabornia* may be excluded from the Chlamydoconchinae by its lack of a mantle which surrounds or encloses the shell. Since it was not possible to determine whether *Parabornia* is monoecious or dioecious or whether it is incubatory, its placement in one of the remaining subfamilies of Thiele's classification may be questioned.

The dioecious Leptoninae possess anterior and posterior differentiated papillae or tentacles and lack papillae ventrally; the shell has, in the left valve, both anterior and posterior teeth and, in the right valve, two anterior and posterior teeth. Clearly, *Parabornia* does not belong to the Leptoninae. The dioecious Galeommatinae have the valves gaping ventrally and the mantle covers part, if not all, of the shell externally. In addition, the galeommatids possess anterior and posterior differentiated papillae or "Taster," and the byssal gland is small. *Parabornia* differs from the Galeommatinae because it has a well-developed, extensive byssal gland, a narrow ventral gape that functions primarily for the passage of the byssus, and a mantle that is retractile into the shell cavity. The remaining group, the Erycininae, appears to be more heterogeneous, but still *Parabornia* differs by definition in that it possesses anterior differentiated papillae.¹ Of all the subfamilies of Thiele, *Parabornia* appears to belong to the Erycininae.

The Erycinidae as defined by Pelseneer (1911) included only *Kellia* and *Lasaea* and are, therefore, more restricted than the Erycininae of Thiele. Thiele did include both *Lasaea* and *Kellia* in his definition of the Erycininae but broadened the definition of the subfamily to include other genera. The Erycinidae, i.e., *Kellia* and *Lasaea* according to Pelseneer, have three pallial openings, namely, a posterior exhalant slit, an anterior inhalant

¹ This characteristic is apparently of little importance, because Thiele described *Ceratomyx* as possessing two anterior and one posterior differentiated papillae, but nevertheless he included it in the Erycininae.

opening, and a pedal-byssal opening. The genus *Parabornia*, with two openings in the mantle, is not closely allied to *Kellia* (= *Tellimya sensu* Thiele) or *Lasaea* (= *Kellya sensu* Thiele). From the other genera that Thiele included in the Erycininae, *Parabornia* also differs, particularly in the characters of the hinge. Of these genera, it may be most closely allied to *Bornia* in its development of the foot and byssal gland, its differentiated papillae, and its reduced outer demibranch. In addition, it has been shown that the muscular system of *Parabornia* is similar to that of *Bornia*, but the latter differs in its hinge configuration wherein the left valve has one large posterior tooth and two smaller anterior ones, while the right valve has one anterior tooth and two elongate posterior teeth.

The placement of *Parabornia* in the Erycininae of Thiele is a concession to our ignorance of the comparative morphology of the Erycinacea. The genus could be placed in Chavan's Montacutidae, but this family appears to be best characterized by its gill structure, which differs radically from that of *Parabornia*. The hinge of *Parabornia* comes close to the type described by Chavan for the group of *Tellimya* that Thiele had included in the Erycininae. Such a situation lends credence to the inclusion of the genus in the Erycininae.

Certainly, more inclusive, detailed, and comprehensive investigations similar to those of Popham (1940) and Deroux (1961) will define the generic and familial units of the Erycinacea and put the taxonomy of the group on a more sound foundation.

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